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SOME PROBLEMS OF TROPICAL PLANT ECOLOGY

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DURING THE LAST SEVEN YEARS there has been in progress a series of phytoecological studies on the warm-humid zones of the lowlands of the Gulf of Mexico. This work has contributed a large quantity of data and many collections of herbarium specimens as a consequence of a systematic sampling carried on in various regions in the lowlands. A detailed presentation of these studies may be found in Gómez-Pompa *et al.* (1964a).

One of the most important points of the methodology is the selection of areas which are arbitrarily limited and are named for some important locality, so that we have the regions of Misantla, of the Tuxtlas, of Córdoba, etc. Once such a region is delimited, a survey is made taking into account and sampling its floristic and environmental variations.

Before explaining the outstanding characteristics and problems of these studies, I wish to discuss some general considerations about certain diverging tendencies which concern ecological studies in tropical zones.

CONSIDERATIONS OF SOME TENDENCIES IN PHYTOECOLOGICAL STUDIES OF TROPICAL ZONES

The basis of the problems and controversies in tropical ecological studies is related to the origin and initial development of plant ecology which occurred in northern extratropical countries and from which we inherited not only a confusing terminology but also a rather dogmatic approach to ecological research. The confusion reached an extreme in usage of terms completely inadequate for the tropical region. An example is the case of the name *tropical rain forest*. This term has no real meaning because there are forests in very rainy areas of the tropics similar to those in temperate areas, such as coniferous forests and deciduous forests which, floristically

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and ecologically are very different from the real "selvas." The selvas are composed of many dominant species of trees and include also lianas, epiphytes and one to several understories of trees. So, the term tropical rain forest causes confusion and when it is translated into Spanish the problem becomes worse. On the other hand, we have the more precise term *selva* which has real meaning but has not been widely accepted in the ecological literature in English.

Since ecological studies began in Europe where the vegetation is mostly altered and the portion conserved in original form is very small, the detailed phytosociological studies of the school of Zurich-Montpellier came into being (Becking, 1957). On the other hand, in the United States with great extensions of vegetation practically unaltered at that time, the school of Clements (1936) with its climax method arose. A very detailed analysis of the origin, development, and method of approach, as well as other aspects of these two lines of ecological thought was presented by Whittaker (1962).

The various methodologies developed in different areas have led to results which at first seem opposed but which, in fact, should not even be compared because of the different emphasis of each. For example, the *monoclimax* of Clements, so severely attacked, does not differ much from the hypothesis of the *polyclimax* of other authors. In relation to this Cain (1947) says: "One is led to wonder to what extent the problem is really one of semantics and only an academic exercise." In fact, much of the discrepancy is due to false interpretation made in good or bad faith by supporters or detractors of the method. Examples are the complex diagrams of the dynamism of the *seres* which some followers of Clements carry out and which Clements himself avoided. The development of the complexity of such problems reaches a point where verification of contrary ideas must be made in the field and not by theoretical discussions, which instead of clarifying each question only bring more confusion to the little which is common among them. For this reason critics of the Zurich-Montpellier school in the United States are unable to establish a basis for their arguments for, as Cain has said (1947) "No American plant association, I believe, has yet been studied thoroughly and throughout its range in the manner of the plant sociologists."

This fact becomes even more serious when we realize that the great majority of the studies on vegetation are made in such a form that their verification is very difficult. This has permitted persons without preparation for this type of work or after only superficial observations to propose "theories" (hypotheses) very difficult to demonstrate.

All these problems have been inherited also in studies of tropical vegetation, but with certain peculiarities which make them even more obvious. Among the problems are: a) the existence of environmental conditions very distinct from those of the extratropical zones; b) a very rich flora in large part unknown; and c) a lack of ecologists, so that, as a result, a large majority of the studies are pursued by botanists of extratropical countries usually on short visits.

From the great quantity of works written concerning the vegetation of the tropics we are able to extract two principal tendencies derived from a fundamental problem in ecology, the concept of the unit in studies of vegetation, or perhaps better, the *association*.

One tendency is that followed by many ecologists who accept definable plant associations, and, although not following the original meaning of Clements (1936) use some of his ideas and terminology. To explain this trend I quote a paragraph from Beard (1955) in his work on the types of vegetation of tropical America, "The basic unit is the plant association which is a floristic grouping, being the largest possible group with consistent dominants either of the same or closely allied species. Associations may be divided into minor floristic groups, to which it was proposed to apply the Clementsian terminology."

The most important of the several schools of ecological thought may be aligned with this tendency. Among them two are outstanding for their influence on studies of tropical vegetation. These are the school of Clements which has been followed in various works on tropical vegetation (Chatterjee 1958; Rosayro 1958; Phillips 1934-1935) and has influenced many others. The second, the school of Zurich-Montpellier, which has had a relatively broad acceptance in many works on various tropical zones (Bharucha 1958; Cuatrecasas 1934; Dilmy & Kostermans 1958; Heyligers 1963; Mangenot 1950-1958).

Although, in fact, the two schools differ so notably they have one point in common which is the recognition of some organization of plant communities.

Within this same tendency we ourselves are able to find a place, that is, we accept artificial units of vegetation as a means and not an end in our studies of vegetation: "The concept of association must be more or less artificial, having the objective of establishing units which permit us to study the whole by means of its parts or having an obvious utility for facilitating our studies." (Gómez-Pompa *et al.* 1964a.)

The second tendency refuses the idea of the organization of these units (Raup 1942). To explain this tendency I quote from Gleason (1939) who has been considered its postulant. "Since every community varies in structure and since no two communities are precisely alike, or have genetic or dynamic connection, a precisely logical classification of communities is not possible. The individualistic concept denies that all vegetation is thus segregated into communities." He considers plant communities as "coincidences" of the individual distribution of the species.

The Gleasonian approach has had a very important effect on vegetation studies in general, but unfortunately this is not so for the tropics. Probably the reason is the inherent difficulty of tropical vegetation. It is interesting to note that Gleason has been badly misinterpreted by many; as he does not deny the existence of associations, one often thinks that his inclusion of them is contradictory. In the work on Puerto Rico, Gleason and Cook (1927) say "In summary it may be repeated that plant associations are the basic units of vegetation, that they are the results of im-

migration and environmental selection, and their duration is short or long, depending on the rate of environmental change. . . . The duty of an ecological survey is to describe these associations, to correlate them with their environment and to discuss their past history and probable future so far as clear evidence exists on which such discussion may be based."

In reality I think that a contradiction does not exist and the fundamental difference is the broad or narrow meaning which different authors have given to the "association"; some have gone very far in the extension of their possible associations and also in their concept, presenting an indefensible point of view. This is, in a way, the case of many followers of Clements and also, in a somewhat different sense that of some phytosociologists. On the other hand, the attitude of denying the existence of associations as some followers of Gleason have done, is rather extreme and denies a fact which, as mentioned earlier, Gleason himself accepts.

My position in regard to this has been that it is difficult to theorize in regard to such problems and that the first thing which must be done, at least in tropical countries, is to study the vegetation and obtain facts and data from which it will be possible to derive ideas and to base some definite position. In other words, it is very difficult to classify without having previously studied the object to be classified. One cannot make a decision without having the data on which to base the decision. In the case of tropical vegetation, in fact, the problem is that very few serious studies have been pursued in an extensive methodical form in the field.

We may wonder why this had happened. I believe that the reason is related to the complex mixture of species in the lowland tropics, added to the fact that the identification of them is extremely difficult because of the poor knowledge of these floras and the very few botanists who can recognize species in the field. The solution to this problem has been made following two main trends, one is related to the study of large samples of a stand using squares of different sizes, this type of work has given very valuable information about floristic composition of rain forests, number of trees per area using local names of species, etc., and the other trend is to present studies of very large areas or countries using just a few species to illustrate some of the groupings.

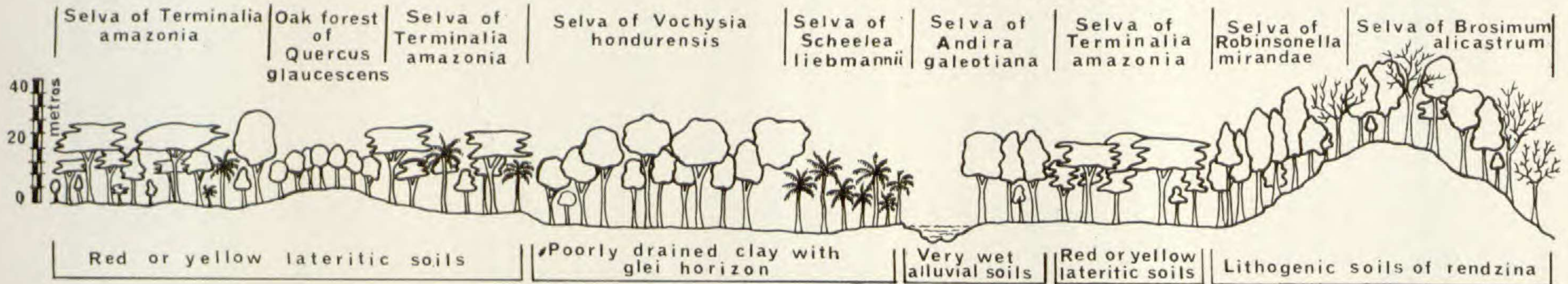
From the studies carried out by us in the warm humid regions of Mexico, it has been possible, I believe, to extract some data which will give an idea of the path to follow in this line of investigation.

PHYTOECOLOGICAL STUDIES IN THE WARM HUMID ZONES OF MEXICO

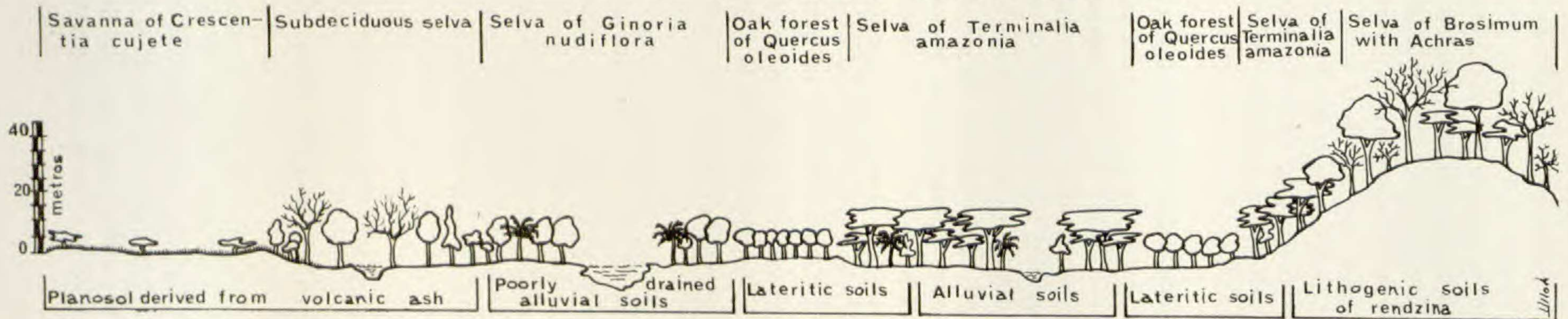
I do not intend in this paper to make an analysis of the studies carried on up to now in these zones, but only to present a series of facts derived from them, which seem to have a basic importance for the understanding of plant communities in the lowland tropics.

1. It is important to acknowledge that in each region or subregion studied there exist groups of species which have "preferences" and include

No. 1 VEGETATION PROFILE FROM TUXTEPEC TO JACATEPEC OAX.



No. 2 VEGETATION PROFILE FROM LOS NARANJOS VER. TO TEMAZCAL OAX.



PROFILE 1 (ABOVE). This profile includes the most important primary plant communities in the area. The rainfall is about 3000 mm. per year and the average of monthly temperatures is 24.8° C. (Redrawn from Gómez-Pompa, Hernández P. & Sousa, 1964b.)

PROFILE 2 (BELOW). This profile includes the most important primary plant communities in the area. The rainfall is about 2300 mm. per year and the average of monthly temperatures is about 25° C. (Redrawn from Gómez-Pompa, Hernández P. & Sousa, 1964b.)

in some cases, strict affinities for certain ecological conditions. For example, in the region of Papaloapan (Gómez-Pompa *et al.*, 1964b) we find a marked contrast in the floristic composition of the limestone hills with the rest of the region occupied mainly by lateritic soils of various types. Even in the lateritic soils we find marked contrasts in the floristic composition according to the topographic variations, internal drainage, and hydromorphism. These contrasts may be drastic or gradual, based on the relationship to the same changes in the local edaphic conditions. A synthetic and diagrammatic profile of a subregion (Tuxtepec-Jacatepec) has been reproduced from the study mentioned above as PROFILE 1.

In the *Brosimum alicastrum* selvas of the limestone hills many species are found which grow only in this type of soil in this area, among them: *Mirandaceltis monoica*, *Mastichodendron capiri* var. *tempisque*, *Protium copal*, *Astronium graveolens*, *Croton* aff. *reflexifolius*, *Sickingia rhodoclada* and many more. This fact is confirmed by other observations, made in many parts of the world, on the importance of calcium as an element in the soil which restricts the entrance of calcifugous species and permits the success of calciphilous species (Jefferies & Willis 1964), although the explanation is obscure especially for warm humid tropical zones.

In the case of the topographic variations within the lateritic soils, however, it should be noted that the floristic differences are less evident among them. Nevertheless, there also exist groups of species with similar patterns of distribution in relation to these edaphic variations.

2. These kinds of affinities or preferences are found not only among "primary" species but also in secondary species (Sousa 1964). This is of great importance inasmuch as in these species there may be found elements of great importance for experimentation on the problems of "preferences."

3. Another fact of interest is that these local patterns of special distribution occur in shrubby and arboreal species in a way perhaps more notable than in other biological forms (vines, herbs, etc.). It is possible that this fact may have become a little distorted because the major emphasis of our studies has been on shrubby and tree species. The most surprising observation is that in a great number of cases the most restricted of such species in certain soil conditions are the most abundant, frequent, and in some cases dominant ones in the environmental condition in which they are found. This fact has an enormous usefulness since it has permitted the use of such species as indicators for cartographic work on a small scale.

It is also notable that if a different region, not very remote, is studied, the whole panorama discussed in the preceding paragraphs may change. It is something of a problem to state exactly why it changes so much because the differences depend upon the area, and vary from region to region. The floristic composition of two regions may be very similar, the ecologically important species may continue to be important but they may "behave" either in a very distinct or in a similar manner. A typical example of this may be seen in the profile of the subregion of Los Naranjos-

Temascal (PROFILE 2), where, in comparison with that of Tuxtepec-Jacatepec, we meet the same important species, as for example *Terminalia amazonia*, found in acid soils on the slopes of the limestone hills, as well as on the margins of arroyos, etc. On the other hand, *Brosimum alicastrum* continues to occupy an important place in limestone soils, so that we may continue analyzing successively the "behavior" of species in the two sub-regions and shall see the whole gamut of change. For example, *Curatella americana*, a species with affinities for the soils of oak woods of Tuxtepec, Oaxaca, is one of the most important arboreal species of the savannas of Los Naranjos, Veracruz, on very different soils.

If the comparison is extended to a more distant region and other species are used the method is similar. For example, in Jacatepec, *Robinsonella mirandae* is typical in calcareous soils and is one of the dominants, but in the region of the Tuxtlas, Veracruz, it is also one of the dominants, here in soils derived from volcanic ash. *Crescentia cujete*, which in the profile of Temascal-Los Naranjos is typical of argillaceous savanna soils (FIG. 1), is found in British Honduras forming an important and typical part of the forests of *Pinus caribaea* on sandy soils (FIG. 2). On the other hand, in this same country *Brosimum alicastrum* is also found on calcareous soils as in our two profiles.

With a basis in these facts, presented in condensed form, we are able



FIG. 1. Savanna with *Crescentia cujete* in Veracruz (see PROFILE 2). Other arboreal species in these savannas are: *Curatella americana*, *Byrsonima crassifolia*, *Coccoloba barbadensis*. *Bromelia karatas* is shown growing at the base of *Crescentia*. These savannas are found in clay soils in flatland areas used mainly for cattle.



FIG. 2. Between Orange Walk and Belize (British Honduras). *Crescentia cujete* can be seen at the edge of the savanna, growing adjacent to the *Pinus caribaea* forest. The palm is *Paurotis wrightii*. These savannas grow in white sandy soils.

to follow the two tendencies explained above, and the decision to follow one or the other will be related to the information used.

1. If considerations are based on the study of only one region or a subregion it is probable that the presence of more or less well defined *patterns of distribution which fall within the strictest limits of the definitions of "association"* can be proven.

2. If several regions are considered and compared, the species studied may present very marked differences in their responses to the diverse ecological situations throughout their range of distribution and may, on this basis, *refute all the definitions of "association."* The independent behavior of each species to the different ecological conditions to which it is submitted in the range of its distribution will make the name, for example, "*selva de Terminalia amazonia*" have no significance.

A difference in basic information seems, therefore, to be the cause of the majority of the discussions on this much debated subject. In relation to this problem I have adopted a position which may, perhaps, conciliate the extremes. This position involves an analysis of the facts in the light of the present botanical knowledge and an effort to explain the apparent discrepancies by taking as a base the species as a fundamental unit and point of departure, as Gleason has done in his individualistic concept.

AN HYPOTHESIS TO EXPLAIN THE FACTS

I believe that in the study of tropical vegetation it is necessary to have more hypotheses to work with, because accumulations of facts as such,

have a limited importance if we do not have some links between them to form some generalized ideas for a better understanding of tropical environments.

When a species is cited from a region as, for example, *Terminalia amazonia* in Chontalpa, Tabasco (FIG. 3), we are dealing, in fact, with a small fragment of the total population of this species, or rather we are dealing with a small fraction of one of the many populations which comprise the species whose total range of distribution covers an area from Brazil to Mexico. This local population is very small considering not only its total distribution, but also the fact that it is a tree species. The gene pool of this population may be very different from that of another population in Panama or in Brazil. The differences between these populations are due to many factors which basically have the effect of discontinuities within the total population of the species.

This phenomenon is very well known and has had a strong influence on taxonomic studies although some taxonomists ignore the concept of the polytypism of species populations. In modern concepts of the species the existence of various populations within one species is taken into account. Mayr (1963) defines the species as "groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups." In consideration of this idea and others having a



FIG. 3. *Terminalia amazonia* selva with its typical stratified treetops, in the state of Tabasco. This selva grows on plains or small hills, on deep, well drained, lateritic soils.

similar focus (Dobzhanski 1941, Huxley 1940), authors tend to call it a biological species concept, and all agree that the species is commonly composed of systems of populations, a theory which is of much interest to us.

Of the possible explanations of discontinuities those of most interest to me are the ones which enable me to establish an explanation for the ecological restriction of certain species to local regions. The most important of those which I have considered may be explained by one example. On many occasions I have had the opportunity to see isolated individuals of tree species which have survived the effects of disturbance in different regions. In the majority of cases these individuals have been undisturbed because of existing shade or because they do not infringe on agricultural or grazing activity (FIG. 4), one of the principal causes of the destruction of the original vegetation. In other situations there are survivors of fires and other disturbances, both artificial and natural (FIG. 5). If such a disturbed zone is abandoned and left to recuperate its vegetation through a secondary succession, it will be noticed that the majority of the plantules of trees which develop will surely come from the mature tree which has persisted. If, in the model we are considering, one (or few) of the trees left belong to the species *Terminalia amazonia*, the future small local population will come from a single tree (in the case of a self-compatible species) or from a few individuals (in the case of self-incompatible species). As a result there is a genetic change which may or may not be morphologically evident depending on the genotype of the parent tree. This phe-



FIG. 4 (LEFT). Isolated tree of *Terminalia amazonia* in a valley near Cordoba, Veracruz. This tree has survived in spite of human disturbance. At the bottom can be seen some selvas growing on limestone. This species is not found in such areas as it grows chiefly on acid soils.

FIG. 5 (RIGHT). Isolated tree of *Terminalia amazonia* near Macal river in British Honduras. This tree has survived a cyclone that threw down most of the trees in the area.

nomenon may be included in some of the distinct types of "genetic drift." This change may be very abrupt depending on the genetic constitution of the parent tree from which a local gene complex will be derived. It may or may not permit the initial population to have characteristics enabling it to compete successfully. An example of this mechanism may possibly be seen in the oak scrub of *Quercus oleoides* (FIG. 6) in the Llanos de Alvarado, Veracruz, a population with an aspect very distinct from the *encinares* of *Q. oleoides* of the neighboring regions (Gómez-Pompa, 1965). These populations resemble the "founder populations" of Mayr (1963) of which he says, "this term (Founder Principle) designates the establishment of a new population by a few original founders which carry only a small fraction of the total genetic variation of the parental population. The descendant population contains only the relatively few genes that the founders have brought with them until replenished by subsequent mutation or by immigration," to which I might add (in the case of plants) that these populations may continue a certain level of gene flow with other populations of the same species, adjacent or distant.

We do not know with certainty that this has happened in the past or that it is happening now; but we know that the majority of so-called virgin forests show evidence of human activity in the past, or at least evidence of fires, inundations, hurricanes, and other catastrophic events which, we may assume, have left some individuals as the basis of future regeneration of the vegetation. Clausen (1962), in reference to such a situation says, "Each local population of a species has probably been started by a limited number of individuals, and it may be effectively isolated from other colonies by spatial isolation."



FIG. 6. Oak scrub of *Quercus oleoides* near Alvarado, Veracruz. This population grows on flat, clay soils, near the coast of the Gulf of Mexico.

Another possible explanation of a similar phenomenon (with a different origin, however) is in the consideration of an area denuded by a catastrophe of nature such as volcanic activity. The material with which the vegetation is reconstructed will be provided in large part by the margins of surrounding species populations. Of all the propagules only those will survive which can compete in and are adapted to the new environment. This could result in a possible change in the new populations. This genetic drift will be more obvious if the surrounding zone presents different edaphic characteristics such as limestone soils, or even different climatic ones. This type of situation may be imagined to have occurred in many zones of the lowlands of the Gulf of Mexico.

As the basis for such a mechanism a quotation from Grant (1963, p. 286) seems pertinent: "In other cases the natural population may be large but has descended from a few migrant individuals. This is often the case in organisms which colonize new areas. A volcano may destroy all traces of pre-existing life on a mountain . . . ; a fire may sweep through a forest; or a tree may simply die of old age, exposing a spot of bare ground. The new ground becomes colonized by migrant plants and animals from surrounding areas. It is not likely that colonizing individuals can bring with them a complete sample of the genetic diversity in the old ancestral population. If the founders of the new population are few in number they could, by chance, represent only one or a few of the genetic variants in the ancestral population from which they came."

These ideas may well explain in part the pronounced response of some shrubby and tree species to certain regional ecological conditions. This is so especially for tropical zones in which the following characteristics are present: (1) that low winter temperature is not the most important limiting ecological factor with which the species has to contend and adapt, as is the case in extra-tropical regions; (2) that natural selection works in these local regions fundamentally in relation to edaphic differences, or rather that the soil plays a very important part in the selection of such individuals in these regions. This fact has been mentioned for different regions in the tropics (Van Steenis 1956). In relation to the soil factor Mason (1946), from his experience in California, says "Of the various categories of environmental factors, the condition of any factor or combination of factors may serve to restrict the range of some species of plants. Of those factors however, the edaphic factor is most apt to occur in sharply defined patterns and often in small areas."

With this hypothesis as a basis, the problem of the distinct behavior of some species from region to region may then be explained.

As noted previously, the possible origin of populations may be different if the parent sources have different genetic constitution. This is more outstanding if we note also that no two areas have the same environmental conditions. We may find environments which are very similar, but into which new factors have entered to produce very strong variation.

The "environment" concept is very complex; nevertheless, in relation

to the behavior of plant species in the Mexican tropics, we can make the following artificial classification.

1. **Highly selective environmental factors.** These factors are relatively independent, such as soils derived from limestone, with different texture and structure; or, poorly drained savanna soils. Several species follow these soils in areas with differing climates and topography. Such is the case of: *Brosimum alicastrum*, *Protium copal*, *Mirandaceltis monoica*, *Mastichodendron capiri* var. *tempisque*, *Trophis racemosa*, *Manilkara zapotilla*, etc., for the limestone areas in many regions of the lowland tropics in Mexico; and of *Curatella americana*, *Crescentia cujete*, *Byrsonima crassifolia* of many savannas of tropical America. Finally, the most extreme type of selective environment is probably the mangrove swamp with a typical floristic composition in many different areas.

2. **Poorly selective environmental factors.** These factors do not imply a great selectivity of species from region to region. The behavior of the species is very variable and seems to depend on variation of independent local factors, such is the case of many different deep, well drained, acid soils. In these soils the following selvas will serve as an example: selvas of *Terminalia amazonia*, *Dialium guianense*, *Pseudolmedia oxyphyllaria*, *Vatairea lundellii*, *Bernoullia flammea*.

Since these are not very selective, the floristic composition and the relative abundance of a single species may vary remarkably from one region to another in relation to still other factors, the most interesting probably being the historical factor. The historical factor may provide the explanation of the origin of the local flora in time and space. Some of these acid soils bear forest which is commonly known as "mixed" rain forest and which seems to have no fixed pattern of species composition, but rather a random dispersal of species. The nutrient mosaics in some of these local areas must play a very important role in such "random" dispersal of species but unfortunately, little is known about these mosaics in the tropics of the New World.

3. **Intermediate factors.** In this category are factors which may be highly selective locally but which are not "followed" by species from region to region, for example, recent alluvial soils. In such soils, characteristic species may be found, but they may differ depending on the region. In this category also two other factors may be included, topography and slope exposure which provoke responses from the species which can be explained only locally. In some cases the variation is very gradual and the responses of the species are equally gradual forming a continuum.

On the basis of this hypothesis we may cite an enormous number of problems needing study which will allow us to open new lines of investigation for the development of plant ecology in the tropics. Among them are:

a). The problem of the experimental initiation of the secondary successions, which will permit us to know something of the modern historical factors and of the behavior of the individuals in these stages. Work of this type has already begun in Mexico (Sarukhán, 1964).

b). The detailed study of the behavior of specific local populations.

c). Work on transplants between populations of the same species coming from different regions, and the initiation of studies of ecotypic differentiation, as well as transplant experiments of species to different environmental conditions from those under which they live. These studies should provide fundamental information for the proposed hypothesis. Also, this type of study could provide the key for resolving the problem of tropical silviculture.

d). The study of breeding systems of the ecologically important species from which may be obtained information about some of the most interesting species. These studies must be complemented, however, with cytogenetical studies permitting extraction of information basic to fundamental problems in ecology and in tropical forest genetics.

Such an approach to the study of tropical plant ecology will remove it from the isolation to which it has been subjected by other sciences, since its problems are related to similar problems in other fields as evolution, taxonomy, population genetics, and so forth. As Mayr (1947) noted "At first sight the concept of geographically and ecologically variable species seems full of contradictions. We see that in one locality a species is restricted to a very definite habitat niche, while in another locality it occurs in a different, sometimes very different niche. We know that through selection in each of these populations a definite gene complex has developed, which permits the population to survive and thrive in spite of competition, predation and all sorts of other adversities."

All the information obtained by the development of genecology, supported by the work of Turesson (1923, 1936), Clausen, Keck, and Hiesey (1940), and more recently by McMillan (1964), Kruckeberg (1951), and Critchfield (1957), is related to such an approach and the impact of the results becomes increasingly stronger because of the same basis of the study, which in the revision of this field by Bennett (1964) is defined as ". . . the study of the genetic mechanisms which operate, within organisms, and between organisms and their environment, at the level both of the individual and of the population, viewed as a process, which at the population level produce those changes known collectively as microevolution."

I think that these studies have to be initiated for tropical plants if we want to get to the basis of the problems.

Surprisingly, the definition of genecology seems to be closely related to the one we proposed for autecology, in which it is limited to "the study and definition of those environmental factors affecting the survival, adaptation, and fertility of the individuals of one species." Since the factors can be defined in broad zones only with difficulty, and since they vary from region to region, we might say that autecology deals with the study of those factors in the macro and microenvironment (as well as the plants) affecting the survival, adaptation and the dynamics of reproduction, of those individuals belonging to one or several regional specific populations. I think it is important to make the comparison between the field of autecology

and genecology because at certain levels there is no great difference, only perhaps a difference of emphasis, as long as both are studied in detail.

All the studies related to these fields are the true basis of synecology. Since in tropical areas such studies scarcely exist, any serious, purely theoretical controversy on tropical vegetation is without basis and must, therefore, await the collection, organization and study of facts and data.

There is a tremendous task in front of us because of our lack of knowledge of tropical plants. We need more and better taxonomic studies of tropical plants, we need also more biological information of them. It is my belief that ecological studies can make a very important contribution to taxonomy if vouchers are mentioned and widely distributed to herbaria. There is great potentiality in the combination of the taxonomy and ecology of tropical plants; there is much to be learned about speciation problems in the tropics and it is my hope that botanists of tropical countries can contribute significantly in this respect.

SUMMARY

1. Most of the studies in tropical plant ecology have been carried on using methods and ideas developed in temperate regions.

2. Controversies have arisen because of very poor field work in the tropics, and because of lack of extensive surveys to prove or disprove some of the ideas.

3. The two apparently opposite ideas, of the existence or absence of clear cut associations in the warm humid tropics, are used to illustrate the confusion existing in tropical plant ecology.

4. An hypothesis to conciliate the two positions in accordance with the facts obtained in studies done in the Mexican tropical lowlands is presented, based on the following factors: a) the edaphic mosaics as a basis of natural selection of local species populations; and b) on the fact that there are not two areas with identical environments; c) on the characteristics of the origin and "behavior" of plant populations in local environments; d) on the natural selection of species populations in local environments as an explanation of the striking patterns of species in these local areas.

5. It is suggested that new methods are much needed in the study of tropical plant ecology and that the evolutionary genecological approach will make a significant contribution to the understanding of the phenomena responsible for what we are finding in vegetation studies in the tropics.

BIBLIOGRAPHY

- BEARD, J. S. 1955. The classification of tropical American vegetation types. *Ecology* 36: 89-100.
- BECKING, R. W. 1957. The Zürich-Montpellier school of phytosociology. *Bot. Rev.* 23: 411-488.
- BENNETT, E. 1964. Historical perspectives in genecology. *Scottish Plant Breeding Station Record* 1964: 49-115.

- BHARUCHA, F. R. 1958. Methods for the study of tropical vegetation. Proc. Kandy Symposium. 89-92. UNESCO.
- CAIN, S. A. 1947. Characteristics of natural areas and factors in their development. Ecol. Monogr. 17: 185-200.
- CHATTERJEE, D. 1958. Tropical vegetation of eastern India. Proc. Kandy Symposium. 61-67. UNESCO.
- CLAUSEN, J. 1962. Stages in the evolution of plant species. Hafner Publ. Co.
- , D. D. KECK & W. M. HIESEY. 1940. Experimental studies on the nature of species. I: Effect of varied environments on western North American plants. Carnegie Inst. Publ. 520: 1-452; II: Plant evolution through amphidiploidy and autopoloidy with examples from the Madiinae. *Ibid.* 564: 1-174.
- CLEMENTS, F. E. 1936. Nature and structure of the climax. Jour. Ecol. 24: 252-284.
- CRITCHFIELD, W. B. 1957. Geographical variation in *Pinus contorta*. Maria Moors Cabot Foundation Publ. 3.
- CUATRECASAS, J. 1934. Observaciones geobotánicas en Colombia. Mus. Nac. Cien. Nat. (Madrid), Trab. Ser. Bot. 27: 1-144.
- DILMY, A., & A. J. G. H. KOSTERMANS. 1958. Research on the vegetation of Indonesia. Proc. Kandy Symposium. 28-32. UNESCO.
- DOBZHANSKY, TH. 1941. Genetics and the origin of species. Columbia Univ. Press.
- GLEASON, H. A. 1939. The individualistic concept of the plant association. Am. Midl. Nat. 21: 92-108.
- & M. I. COOK. 1927. The plant ecology of Porto Rico. Sci. Surv. of Porto Rico and the Virgin Isl. 7.
- GÓMEZ-POMPA, A. 1965. La vegetación de México. Bol. Soc. Bot. México 29: 76-120.
- , J. VÁZQUEZ SOTO & J. SARUKHÁN K. 1964a. Estudios ecológicos en las zonas cálida húmedas de México. Publ. Esp. Inst. Nac. Inv. For. México 3: 1-36.
- , L. HERNÁNDEZ P. & M. SOUSA S. 1964b. Estudio fitoecológico de la cuenca intermedia del Río Papaloapan. Publ. Esp. Inst. Nac. Inv. For. México 3: 37-90.
- GRANT, V. 1963. The origin of adaptations. Columbia Univ. Press.
- HEYLIGERS, P. C. 1963. Vegetation and soil of white-sand savanna in Surinam. Meded. Bot. Mus. Utrecht 191: 1-148.
- HUXLEY, J. S. 1940. The new systematics. Clarendon Press.
- JEFFERIES, R. L., & A. J. WILLIS. 1964. Studies on the calcicole-calcifuge habit. I. Methods of analysis of soil and plant tissues and some results of investigations on four species. Jour. Ecol. 52: 121-138.
- KRUCKEBERG, A. R. 1951. Intraspecific variability in the response of certain native plant species to serpentine soil. Am. Jour. Bot. 38: 408-419.
- MANGENOT, G. 1950. Essai sur les forêts denses de la Côte d'Ivoire. Bull. Soc. Bot. France 97: 159-162.
- . 1958. Les recherches sur la végétation dans les régions tropicales humides de l'Afrique Occidentale. Proc. Kandy Symposium. 115-126. UNESCO.
- MASON, H. L. 1946. The edaphic factor in narrow endemism. I. The nature of environmental influences. Madroño 8: 209-226.
- MAYR, E. 1947. Ecological factors in speciation. Evolution 1: 263-288.
- . 1963. Animal species and evolution. Harvard Univ. Press.

- McMILLAN, C. 1964. Survival of transplanted *Cupressus* and *Pinus* after thirteen years in Mendocino County, California. *Madroño* 17: 250-253.
- PHILLIPS, J. F. V. 1934-5. Succession, development, the climax, and the complex organism: An analysis of concepts. Parts I-III. *Jour. Ecol.* 22: 554-571; 23: 210-246, 488-508.
- RAUP, H. M. 1942. Trends in the development of geographic botany. *Ann. Assoc. American Geographers* 32: 319-354.
- ROSAYRO, R. A. DE. 1958. Tropical ecological studies in Ceylon. *Proc. Kandy Symposium*. 33-39. UNESCO.
- SARUKHÁN, K., J. 1964. Estudio sucesional de un area Talada en Tuxtepec, Oaxaca. *Publ. Esp. Inst. Nac. Inv. For. México* 3: 107-172.
- SOUSA, S., M. 1964. Estudio de la vegetación secundaria en la región de Tuxtepec, Oaxaca. *Publ. Esp. Inst. Nac. Inv. For. México* 3: 91-105.
- STEENIS, C. G. G. J. VAN. 1956. Basic principles of rain forest sociology. *Proc. Kandy Symposium*. 159-165. UNESCO.
- TURESSON, G. 1923. The scope and import of genecology. *Hereditas* 4: 171-176.
- . 1936. Rassenökologie und Pflanzengeographie. *Bot. Not.* 3-4: 420-437.
- WHITTAKER, R. H. 1962. Classification of natural communities. *Bot. Rev.* 28: 1-239.

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